The scaling of eye size with body mass in birds

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We developed a simple method that uses skulls to estimate the diameter, and hence the mass, of birds' eyes. Allometric analysis demonstrated that, within five orders (parrots, pigeons, petrels, raptors and owls) and across 104 families of flying birds, eye mass is proportional to (body mass)$^{0.68}$ over a range of body masses (6 g–11.3 kg). As expected from their habits and visual ecology, raptors and owls have enlarged eyes, with masses 1.4 and 2.2 times greater than average birds of the same weight. Taking existing relationships for flight speed on body mass, we find that resolution increases close to (flight speed)$^{1.333}$. Consequently, large birds resolve objects at a longer time to contact than small birds. Eye radius and skull size co-vary in strict proportion, suggesting common physiological, aerodynamic and mechanical constraints. Because eye mass scales close to brain mass, metabolic rate and information processing could also be limiting, but the precise factors determining the scaling of eye to body have not been identified.

Keywords: visual ecology; eye; resolution; flight speed; body mass; allometry

1. INTRODUCTION

Birds have large eyes relative to body mass and this is thought to be an adaptation to rapid flight (Walls 1942; Martin 1985). For simple eyes operating in bright light, spatial resolution (the reciprocal of the smallest resolvable angle) increases in proportion to focal length. Thus, an increase in the axial length or radius of the eye extends the distance at which an animal can resolve a given object. This extended range is beneficial to a fast-moving animal, because it must resolve obstacles, navigate and use resources over greater distances. This simple line of argument supports Leuckart's law—swifter moving animals have larger eyes (Hughes 1977)—and predicts that spatial resolution and, hence, eye length should increase in proportion to speed.

How plausible is a scaling of eye length to speed? In many groups of animals both the size of the eye and the speed of locomotion increase with body size. Contrary to a suggestion by Kirschfeld (1976), eyes do not scale to provide a resolution that is proportional to body height. For simple eyes, such as those of birds and mammals, Kirschfeld's (1976) suggestion requires isometric scaling of eye to body, but the relative size of the eye declines as body mass increases (Hughes 1977). The number of body lengths that an animal moves per unit time also tends to decrease as body size increases. Consequently, a scaling of the eye to the speed of locomotion provides a plausible explanation for the decline in the relative size of the eye with increasing body mass.

Given the relative paucity of hypotheses and published data on eye scaling in vertebrates, we have used birds to test the proposition that eyes enlarge with body weight to increase spatial resolution in proportion to speed. Birds were chosen because their large eyes suggest that vision is an important modality, subject to considerable selective pressure (Walls 1942; Martin 1985; Thomas 1999). In addition, aerodynamics predict (Norberg 1990) that the flight speed of birds with similar body plans increases as (body mass)$^{0.167}$. Because spatial resolution is proportional to focal length (Kirschfeld 1976; Hughes 1977; Martin 1983, 1985), to provide a resolution that is proportional to flight speed the lineal dimensions of the eye (radius, diameter and axial length) should scale as (body mass)$^{0.167}$ and eye mass should scale as (body mass)$^{0.5}$. To test this prediction we developed a simple method for estimating eye diameter from the skulls of birds whose body weights are tabulated.

2. METHODS

Since fresh eyes from an adequate variety of species were not available, we devised the following technique to estimate eye diameter. A spherical ball of Plasticine was prepared by hand and its size adjusted until it fitted comfortably into the eye socket of a fleshless skull. In this context, 'comfortably' implies that the ball could fit into the socket without touching any part of the skull while the gap between bone and ball on the median side was *ca.* 1 mm. The diameter of this ball was used to estimate the eye mass of the species, assuming the eye was also spherical and had a density of 1 g cm^{-3}.

To validate this technique, we first compared the measurements obtained from Plasticine with those published elsewhere for several species on which detailed studies have been undertaken. We also made use of eyes from 12 species collected during other studies (Hayes & Brooke 1990; Hayes *et al.* 1991) on the visual ecology of various species of petrels and albatrosses (Procellariiformes). The eyes were fresh since the birds had suffered such mishaps as flying into buildings. Eleven species were obtained for the South Atlantic island of Gough and the

Proc. R. Soc. Lond. B (1999) **266**, 405–412
Received 27 October 1998   *Accepted* 20 November 1998

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12th was the Manx shearwater *Puffinus puffinus*, from the island of Skomer off the coast of Wales. The corneoscleral junction diameter and the axial length of each eye was measured (Martin & Brooke 1991). Based on between 2 and 22 eye measurements for each species, the species' mean corneoscleral diameter and mean axial length were then correlated with the eye diameter as estimated from the Plasticine technique described above.

The main source of skulls for the study was the University Museum of Zoology, Cambridge. The birds in this collection are classified according to Peters' (1931–1986) catalogue and, therefore, this classification was used during the museum work. To look at the scaling of the eye across all birds, one suitable specimen per extant bird family was selected at random from the collection and the eye diameter and mass estimated. The masses of these bird species were primarily obtained from Dunning (1993), with supplementary information from Cramp *et al.* (1977–1994) and del Hoyo *et al.* (1992–1997). Where these sources gave a range rather than a mean, the midpoint was used.

To investigate whether eye diameter and mass scaled similarly within orders, as across the generality of birds, five orders of birds were selected for more detailed study. These were as follows.

(i)   The Psittaciformes or parrots, a structurally uniform, terrestrial group whose plant diet and diurnal lifestyle (no nocturnal or flightless parrots included) do not obviously demand special visual adaptations.

(ii)   The Columbiformes or pigeons (excluding sandgrouse) for the same reasons as for the Psittaciformes.

(iii)   The Procellariiformes, the seabirds used in the validation study and also a group whose members span an exceptional size range of almost three orders of magnitude.

(iv)   The Falconiformes, excluding the New World vultures whose affinities are debated (Sibley & Ahlquist 1990; Siegel-Causey 1997), since birds of prey may require special visual adaptations.

(v)   The Strigiformes or owls which are not only predatory but also nocturnal.

For one random individual per species, we estimated eye diameter and mass for all the species from the five orders available in the Cambridge Museum. However, the museum's holding is not large. To enhance the sample size, we also visited the Natural History Museum, Tring and estimated eye diameter and mass for those additional species for which Dunning (1993) provided body masses. No species was used both in this part of the study and in the general investigation of scaling across many orders.

There continues to be debate over whether such allometric analyses should treat each species as an independent data point or whether the calculation of contrasts within a phylogenetic framework is more appropriate (Harvey & Pagel 1991; Martin 1996; Ricklefs & Starck 1996). For our analyses of allometric scaling of eye mass on body mass, we adopted both approaches. When assuming independence, there is the possibility of error in the determination of body mass, i.e. the *x*-variable in our and many comparable studies of allometric scaling. In this context there has been discussion as to whether model I or model II regression is the most appropriate technique (Rayner 1985; Sokal & Rohlf 1995; Weathers & Siegel 1995; Ricklefs 1996). Since the error rate in our measurement of the *x*-variable, a mean body mass from literature, is probably less than one-third of the error in the

Table 1. *Diameters of bird eyes determined by the present Plasticine technique and axial lengths reported in the literature*

(Both measurements in millimetres.)

species	diameter	axial length
Struthio camelus	37.0	39.0[a]
Puffinus puffinus	14.7	11.8[b]
Aquila audax	32.5	33–36[c]
Strix aluco	23.0	29.0[a], 35.7[d]
Columba livia	16.0	11.6[a,d]

[a] Martin & Katzir (1995).
[b] Martin & Brooke (1991).
[c] Reymond (1985).
[d] Martin (1998).

measurement of the *y*-variable, eye mass, we have used least-squares regression (model I) to determine the allometric exponent of log(eye mass) on log(body mass). This procedure is considered acceptable (Rayner 1985; Weathers & Siegel 1995) and the values so derived form the basis of our discussion. However, we also provide the regression slopes based on reduced major axis analysis (model II) later in table 2. In the text and figures all logarithms are to base 10.

When working within a phylogenetic framework, contrasts were calculated using the CAIC 2.0.0 program (Purvis & Rambaut 1995) and the phylogeny of Sibley & Ahlquist (1990). For the between-families analysis, it was possible either to assume equal branch lengths or to calculate branch lengths from the $\Delta T_{50}H$ values provided by Sibley & Ahlquist (1990). The phylogeny is less well resolved within orders and, therefore, for the five within-order analyses, we simply assumed equal branch lengths.

To relate eye size to skull size excluding bill, we measured skull length as the distance between the occipital condyle and the pterygopalatine joint and width as the distance between the left and right temporal fossae. Skull measurements were made of almost all specimens where eye size was estimated.

3. RESULTS

For the 12 species of albatross and petrel, whose masses ranged from 47 g to 2.5 kg, eye diameter, as measured by our Plasticine technique, correlated highly with the axial length of the fresh eye ($r^2 = 0.958$ and $p < 0.0001$). The slope of the regression of plasticine eye diameter on axial length was 1.006 ($\pm$s.e. 0.064). Importantly for the present scaling study, this slope was not significantly different from one and, thus, there was no size-related change in the relationship between Plasticine eye diameter and axial length. We also compared the eye diameter that we determined with reliably determined axial lengths reported in the literature (table 1). The correspondence is also close. Not surprisingly, the Plasticine method tends to overestimate the axial length of species with flattened eyes (e.g. *Columba livia*) and underestimate the axial length of species with tubular eyes (e.g. *Strix aluco*). Overall we used the Plasticine technique with confidence.

Eye diameter, as measured by our Plasticine technique, also correlated highly with the corneoscleral diameter ($r^2 = 0.883$ and $p < 0.0001$), but the slope of the regression of Plasticine eye diameter on corneal diameter
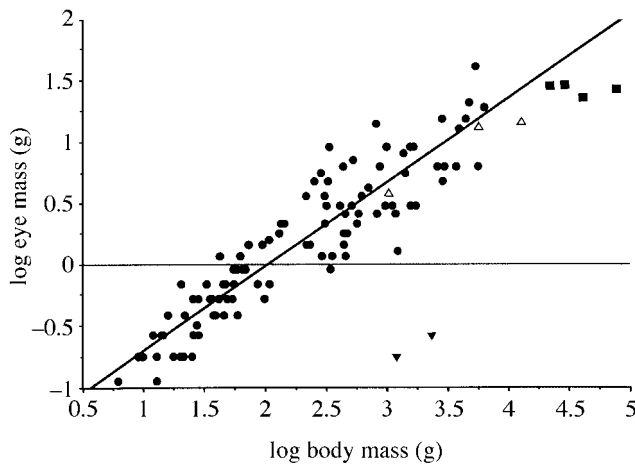
Figure 1. The regression of eye mass on body mass for 104 species of flying birds, each from a different family. $y = 0.682x - 1.379$, $r^2 = 0.846$ and $p < 0.0001$. Slope of reduced major axis regression = 0.741. Although not included in the calculation of the regression, nine non-flying birds are also shown, two kiwis (*Apteryx* spp.; ▼), three penguins (Spheniscidae; △) and four large ratites (■)

Table 2. *The scaling exponent of eye mass on body mass derived for five bird orders using different analytical techniques*

(Standard errors and sample sizes for the model I and model II regressions, using species as independent points, are the same (Sokal & Rohlf 1995). s.e. and n are in parentheses.)

	model I regression		
	species as independent points	phylogenetically independent contrasts	model II regression
Psittaci-formes	0.828 (0.102: 22)	0.863 (0.150: 6)	0.946
Columbi-formes	0.673 (0.107: 19)	0.631 (0.396: 5)	0.805
Procellarii-formes	0.848 (0.066: 15)	0.571 (0.107: 5)	0.881
Falconi-formes	0.730 (0.078: 20)	0.872 (0.129: 6)	0.769
Strigi-formes	0.656 (0.082: 15)	0.845 (0.236, 5)	0.720

(1.891 ± 0.206) was significantly greater than one $(t = 4.33$, d.f. = 10 and $p < 0.002)$, suggesting that larger eyes had relatively smaller corneas.

Amongst the generality of flying birds, representing one species from each of 104 families and, therefore, rather more than half the families of birds, the scaling exponent of eye mass on body mass was 0.682 ± 0.029 (figure 1) when each taxon was treated independently. Using phylogenetically independent contrasts (PICs), the value was 0.696 ± 0.037 $(n = 69)$ when branch lengths were not edited and 0.691 ± 0.036 $(n = 69)$ when they were. The species in these analyses cover a 2000-fold range of body mass, from the 6 g Australian warbler *Acanthiza pusilla* to the 11.3 kg Andean condor *Vultur gryphus*. Figure 1 also shows measurements for nine species of non-flying birds that were not included in the determi-

nation of scaling factor. As is well known, the eyes of nocturnal kiwis (*Apteryx* spp.) are exceptionally small for birds of their body mass (Walls 1942). The three penguin species (family Spheniscidae) plot close to the line for flying birds. The four large non-flying ratites, namely the rhea (*Rhea macrorhnycha*), ostrich (*Struthio camelus*) and cassowaries (*Dromaius novaehollandiae* and *Casuarius casuarius*), are among the largest living birds. Their eyes are somewhat smaller than predicted by the regression for flying birds.

Using individual taxa, the scaling exponents for eye mass on body mass for parrots (figure 2a) and pigeons (figure 2b) were 0.828 ± 0.102 and 0.673 ± 0.107, respectively, in neither case significantly different from that of all flying birds. Both groups plot close to the regression for flying birds shown in figure 1. Petrels and albatrosses also plot close to the general regression (figure 2c), but eye mass appears to increase more rapidly with body size. However, the petrel–albatross scaling exponent (0.848 ± 0.066) is not significantly greater than the value for all birds $(t = 1.68$, d.f. = 115 and $0.05 < p < 0.1)$.

While the scaling exponents of eye mass on body mass for birds of prey (figure 2d) and owls (figure 2e), 0.730 ± 0.078 and 0.656 ± 0.082, respectively, were not significantly different from that of all flying birds, both groups have larger eyes than would be expected for their body size. Thus, the elevations of both the bird of prey $(t = 4.90$, d.f. = 121 and $p < 0.001)$ and owl $(t = 4.41$, d.f. = 116 and $p < 0.001)$ regressions are significantly above the regression for flying birds and, indeed, all measured birds of prey and owls plot above that regression (figure 2d and 2e).

For each of the five orders, we also calculated the scaling exponent using PICs (table 2). With the single exception of the pigeon value of 0.631, all the PIC values were significantly above zero $(p < 0.05)$. However, none differed significantly from the value calculated using each taxon as an independent point. In this respect our findings are in accord with other allometric regression studies where regressions based on individual taxa and phylogenetic contrasts generally produced similar results (Ricklefs & Starck 1996). Table 2 also provides the results of the model II reduced major axis analysis (see §2).

For flying birds, eye size is directly proportional to skull size. The regression of eye diameter on skull width is diameter = 0.671 width + 0.828 $(n = 110$, s.e. of slope ± 0.033, $r^2 = 0.788$ and $p < 0.0001)$. The regression of eye diameter on skull length is diameter = 0.755 length + 4.367 $(n = 90$, s.e. of slope ± 0.041, $r^2 = 0.79$ and $p < 0.0001)$. However the relationship between eye size and skull size is different to this for the two groups with unusually large eyes: the birds of prey and the owls.

For a given skull width, birds of prey tend to have larger eyes than birds in general (figure 3a) but the difference is not significant $(t = 1.53$, d.f. = 106 and $p > 0.1)$. However, for a given skull length, the eyes of birds of prey are significantly larger (figure 4a) than those of flying birds $(t = 7.53$, d.f. = 106 and $p < 0.001)$. Note that neither the slope of the linear regression of eye diameter on skull width $(0.696 \pm 0.138$, figure 3a) nor of eye diameter on skull length $(0.923 \pm 0.150$, figure 4a) is significantly different from that for flying birds.

The pattern of change in eye diameter with skull size is different among owls. Eye diameter barely increases with
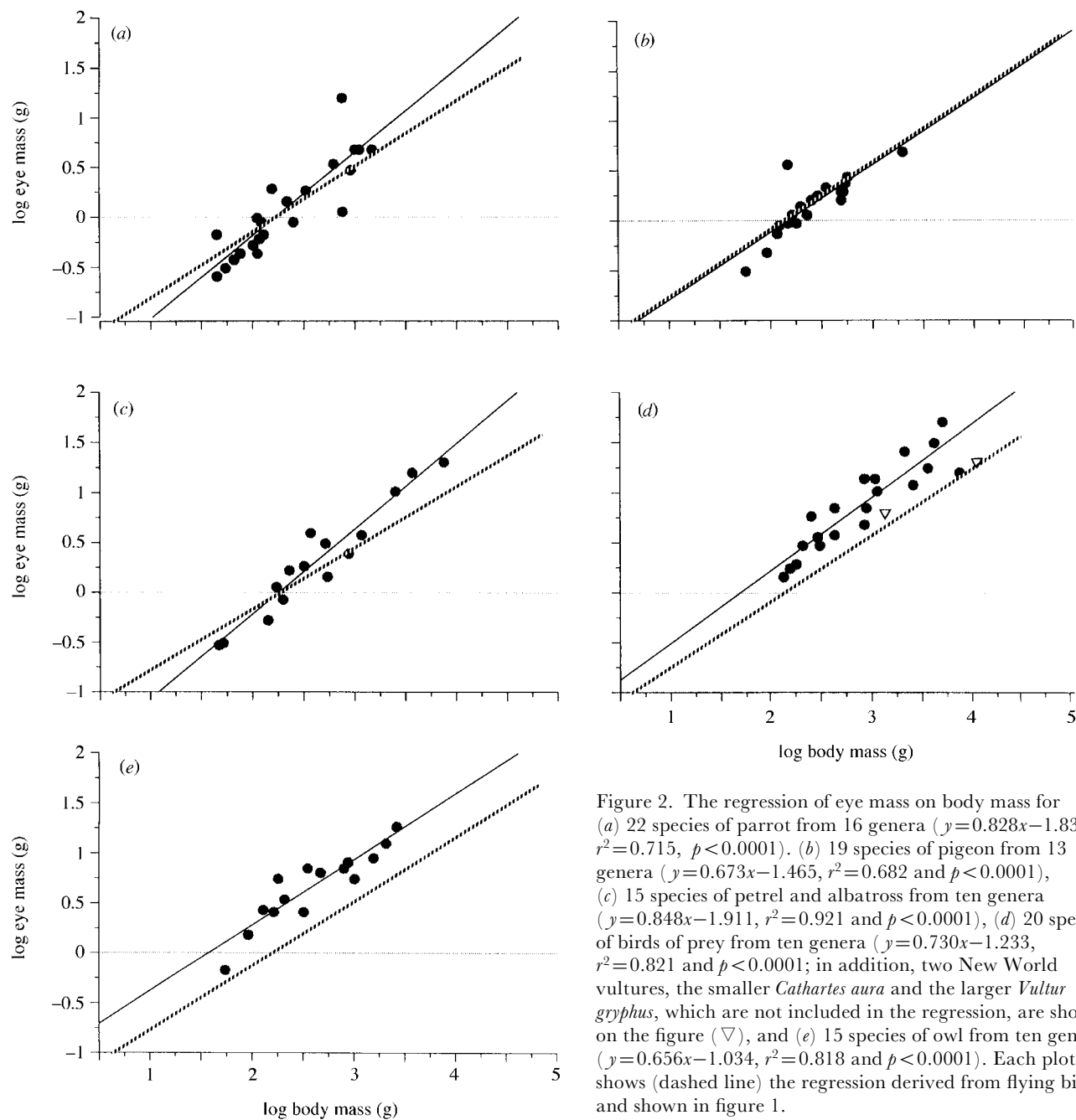
Figure 2. The regression of eye mass on body mass for
(*a*) 22 species of parrot from 16 genera ($y=0.828x-1.839$, $r^2=0.715$, $p<0.0001$). (*b*) 19 species of pigeon from 13 genera ($y=0.673x-1.465$, $r^2=0.682$ and $p<0.0001$), (*c*) 15 species of petrel and albatross from ten genera ($y=0.848x-1.911$, $r^2=0.921$ and $p<0.0001$), (*d*) 20 species of birds of prey from ten genera ($y=0.730x-1.233$, $r^2=0.821$ and $p<0.0001$; in addition, two New World vultures, the smaller *Cathartes aura* and the larger *Vultur gryphus*, which are not included in the regression, are shown on the figure ($\triangledown$), and (*e*) 15 species of owl from ten genera ($y=0.656x-1.034$, $r^2=0.818$ and $p<0.0001$). Each plot also shows (dashed line) the regression derived from flying birds and shown in figure 1.

skull length among owls (figure 4*b*). The slope of the regression, 0.111 ± 0.152, is not significantly different from zero. However, the slope is significantly less than that for all flying birds ($t=5.99$, d.f.$=101$ and $p<0.001$). Eye size also increases only modestly with increasing skull width (figure 3*b*). In this case the slope, 0.262 ± 0.071, is significantly greater than zero ($p<0.005$). It is also significantly less ($t=5.96$, d.f.$=123$ and $p<0.001$) than the slope for flying birds. Thus, it appears more likely that owls have evolved wide skulls to facilitate hearing (Payne 1971) than to accommodate large eyes.

4. DISCUSSION

(a) *Spatial resolution and flight speed*

Is the spatial resolution of a bird's eye proportional to its flight speed? Retinal magnification and, hence, spatial resolution increase in proportion to the axial length of the eye (Kirschfeld 1976; Hughes 1977; Martin 1985). Current studies indicate that flight speed increases as (body mass)$^{0.167}$ (Norberg 1990). To increase in linear proportion to speed, eye length should scale with the same exponent (0.167), so causing eye mass to scale with an exponent of 0.5. Across 104 extant families and a 2000-fold range of body weights we found that

$$\log(\text{eye mass}) = 0.68\ \log(\text{body mass}) - \log(23.9).$$

The exponent in this allometric function, 0.68, is close to 0.67, suggesting that spatial resolution scales as (body mass)$^{0.67 \times 0.33}$ and, hence, as (flight speed)$^{1.33}$. Therefore, large birds will resolve objects at a longer time to contact than small birds. This finding does not contradict the suggestion (Walls 1942; Martin 1985) that flight contributes
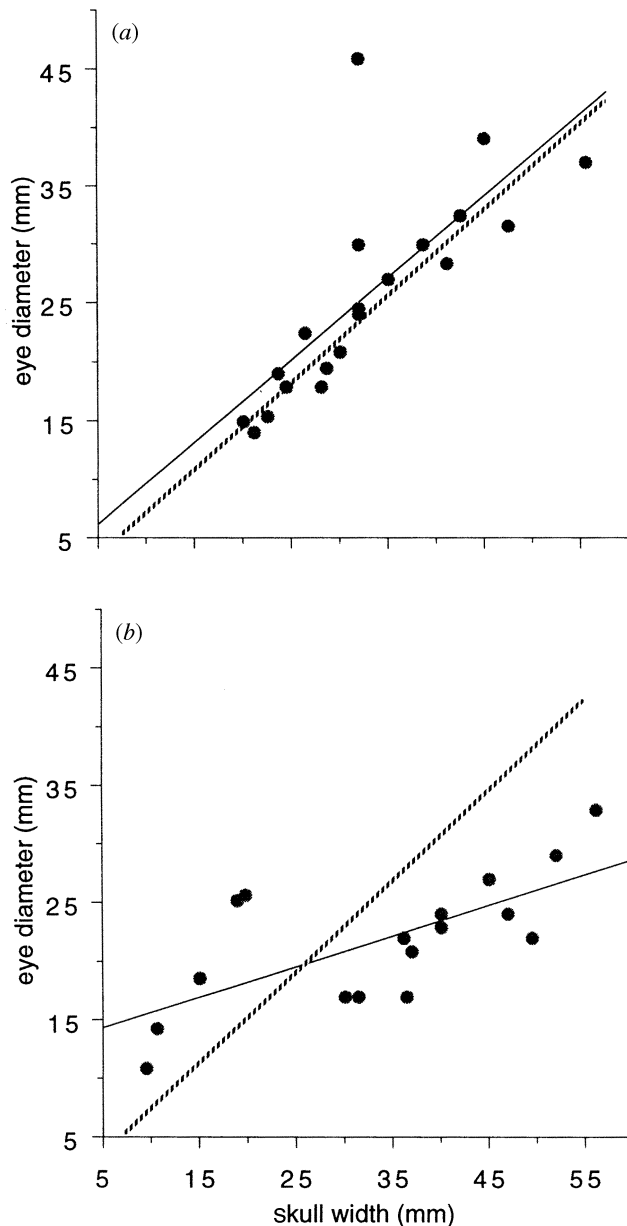
Figure 3. The regression of eye diameter on skull width for (*a*) 20 species of birds of prey ($y = 0.696x + 2.734$, $r^2 = 0.560$ and $p < 0.0001$), and (*b*) 17 species of owl ($y = 0.262x + 12.984$, $r^2 = 0.440$ and $p < 0.005$). Each plot also shows (dashed line) the regression derived from flying birds.

Figure 4. The regression of eye diameter on skull length for (*a*) 19 species of birds of prey ($y = 0.923x + 8.084$, $r^2 = 0.672$ and $p < 0.0001$), and (*b*) 15 species of owl ($y = 0.111x + 20.035$, $r^2 = 0.034$ and n.s.). Each plot also shows (dashed) the regression derived from flying birds.

to the relatively large size of birds' eyes. Indeed, we support this proposal by noting that flightless birds tend to have smaller eyes than flying birds of the same body weight (figure 1).

The rejection of the proposition that resolution is linearly proportional to flight speed depends on three provisos: (i) our measure of eye diameter represents spatial resolution, (ii) flight speed increases as (body mass)$^{0.167}$, and (iii) we have derived the correct scaling exponent for eye on body.

Consider the first proviso, our measure of eye diameter as a predictor of resolution. The method, fitting a Plasticine sphere into the orbit of the skull, estimates axial length reliably. There is a strong correlation between the estimates made from skulls and fresh specimens and our measure of diameter agrees with independent measures of
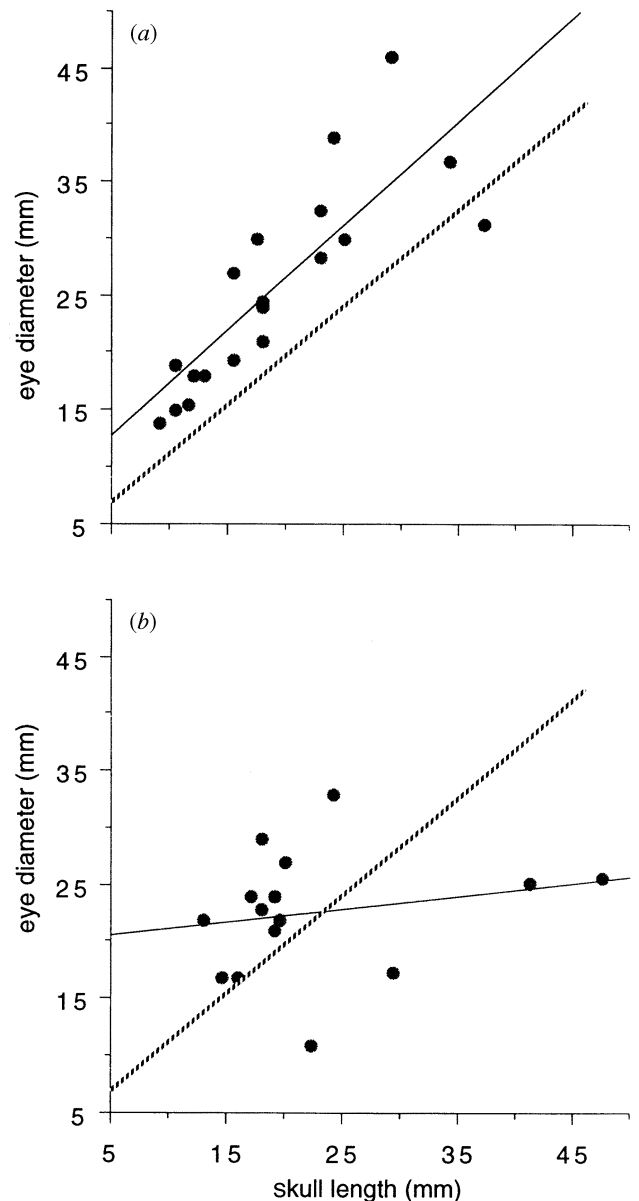
axial length (table 1). For simple (camera-type) eyes of the same shape, resolution increases in proportion to focal length (Kirschfeld 1976) and focal length is proportional to other reliable measures of lineal dimensions, such as corneal radius (Howland *et al.* 1997). The fitting of a regression line to data from 104 families will tend to remove the effects of the differences in eye shape found in birds (Martin 1985). Thus, our simple technique provides a reasonable approximation of the resolving power and will generate the correct scaling exponent. The technique has an extra advantage. By using skulls from existing collections, one can measure a wide variety of birds without obtaining freshly killed specimens.

Now consider the second proviso, flight speed increases as (body mass)$^{0.167}$. This theoretical relationship is derived from the basic aerodynamics of flight and is supported by

a limited amount of empirical data, drawn from a variety of birds (Rayner 1988; Norberg 1990, 1996). The theory applies to birds that have the same shaped bodies (i.e. have identical corresponding angles) and we examined scaling within families whose members have similar body shapes. Each of the five families had a different body plan and in none did the scaling exponent differ significantly from birds in general. In a study of passerine birds, Thomas (1999), using different measuring methods, found a scaling exponent of 0.771 (95% confidence interval 0.665–0.877) and, therefore, not significantly different to our results. Together these controls suggest that changes in body shape have little effect on the scaling exponent for eye mass. However, it has been suggested (Norberg 1996) that, because of morphological changes, the speeds for minimum power consumption and maximum range increase as (body mass)$^{0.21}$. If this suggestion is correct and minimum power and maximum range are the relevant speeds, eye masses are scaling with a resolution that is nearly proportional to flight speed (the measured exponent of 0.68 is close to the required exponent of 0.63). A comparison of eye size in species whose relevant flight speeds are known would resolve this uncertainty but, at present, there are insufficient flight data (Pennycuick 1997).

Finally, consider our third proviso, that our statistical treatment of our data generates the correct scaling exponent. Two possible sources of error are well recognized. First, the correct scaling relationship can be lost by pooling data points from many taxonomic groups because, although the points within each group fall on a line with the correct slope, each group's line has a unique origin that reflects the relative eye size that is characteristic of that group (e.g. raptors as compared to birds in general in figure 2). This unique property of the group displaces their points laterally. The use of data points from many different groups, each subject to a different lateral shift, can bias the distribution and generate an incorrect exponent (Martin 1996). Our analysis of data from within orders controls against this type of error. Importantly, the scaling exponent within orders is not significantly different from the exponent across 104 families, even though the relative size of the eye varies between these families. A second source of error could be the bias introduced by phylogenetic constraints (Harvey & Pagel 1991; Martin 1996). However, correcting for this possible bias using independent contrasts (Purvis & Rambaut 1995) made no significant difference to our results (table 2). Moreover, we found the more closely related members of single orders scale with the same exponent as the individual representative from 104 families, again suggesting that phylogenetic effects are small.

(b) The scaling of eye size to body size in birds and other vertebrates

On an allometric plot of log(eye length) versus log(body mass) (Hughes 1977, fig. 9a), the points for 'all vertebrates', from small birds, mammals and fishes to elephants and whales, are scattered across a trajectory whose slope decreases steadily with increasing body mass, suggesting that eye length increases as the logarithm of body mass (Hughes 1977; Howland & Merola 1993). The

eyes of very small vertebrates, such as the smallest rodents, appear to scale with an exponent close to 1. As body mass increases, the exponent steadily declines and eye size asymptotes to an axial length between 35 and 50 mm. The eyes of the ostrich, eagle, zebra, giraffe, elephant and baleen whale are all in this size range, leading Hughes (1977, p. 653) to observe that 'given the nature of the elements common to its construction and the physical world to which it is adapted, a globe from 35 mm to 50 mm diameter suffices to meet the most stringent requirements of species over a 10^4-fold range of body size'.

The remarkable feature of eye scaling in birds is its apparent uniformity over a wide range (figure 1), from 6 mm in the 6 g Australian warbler *A. pusilla* to 46 mm in the 4.9 kg eagle *Haliaetus albicilla*, a similar total range to that reported by Walls (1942). However, unlike the data for vertebrates in general, there is no clear decline in scaling exponent as birds approach the upper limit of eye size. If our data for 104 families of flying birds are divided arbitrarily at 100 g, then the scaling exponent for birds weighing $\leqslant 100$ g is 0.804 ± 0.080 ($n=47$) while the exponent for flying birds weighing >100 g is less, 0.559 ± 0.076 ($n=57$), but not significantly so. Studying European passerines, mostly weighing <100 g, Thomas (1999) found a scaling coefficient of 0.771. Such uniformity suggests that there are similarities between the patterns of cost and benefit that determine the level of investment in vision in birds of all sizes.

Existing allometry fails to demonstrate that these patterns of constraint are unique to birds. Our scaling exponent for eye diameter against body mass in birds (0.23) lies between the value of 0.19 derived for a smaller sample of 71 bird species (Howland & Merola 1993; H. C. Howland, personal communication) and the value of 0.27 obtained from 21 species of tropical amphibia (Howland *et al.* 1997) with body masses similar to birds (1 g–1 kg). Unpublished data suggests that rodents have smaller eyes than amphibia, but scale with a similar exponent (quoted in Howland *et al.* (1997)). Birds' eyes are apparently scaling with an exponent that is similar to other vertebrates of the same mass but data from birds and other vertebrate groups are required to substantiate this observation.

(c) Specializations of birds' eyes

Birds have relatively large eyes and, in line with Leuckart's law, this helps them to cope with the increase in speed and range provided by flight (Walls 1942; Hughes 1977; Martin 1985). This observation is not contradicted by our finding that resolution does not scale linearly with flight speed. However, speed is not the only determinant of eye size. Ecology and behaviour are also significant. The allometric equation for raptors shows that their eyes are 1.4 times bigger than those of 'average' birds of the same mass and, in conjunction with the extension in effective focal length provided by their deep foveal pit (Snyder & Miller 1978), this provides a high level of acuity that aids prey detection. Owls' eyes are also larger, by a factor of 2.2 (figure 2e), to provide a wide pupil that improves sensitivity for night vision (Martin 1983, 1985). The slightly larger exponent of petrels suggests that other ecological and phylogenetic factors could also influence

scaling. A more detailed comparison of scaling in particular groups could well reveal further adaptations of the bird eye to particular aspects of behaviour and visual ecology, such as the size of preferred food items, habitat and diurnal activity cycle (Thomas 1999).

(d) *Factors that constrain the size of a bird's eye*

The scaling exponent for eye mass on body mass in birds, 0.68, is close to 0.67, but the explanation for this apparently simple relationship is not clear. We have considered a number of factors. All can be associated, to a greater or lesser extent, with the mass of the eye, but none provides a complete explanation. The first factor is metabolic rate. Eyes are metabolically expensive because the retina has a high specific metabolic rate and eyes constitute a considerable proportion of body mass. At the taxonomic level of families within orders, metabolic rate scales against body mass with an exponent of 0.67 (Bennett & Harvey 1987). Although this value is almost identical to our exponent for eye mass, one should not conclude that metabolic rate directly determines the size of a bird's eye. The exponent for metabolic rate increases when one descends to lower taxonomic levels but, in our five cases (figure 2), we did not observe statistically significant increases in the exponent for eye mass within orders. More data on eye mass are required to establish a strict correlation between eye mass and metabolic rate. In addition, metabolic rate is unlikely to be the sole limiting factor.

A second factor is the mass of the brain. For birds in general, the scaling exponent for brain mass on body mass ranges from 0.5 to 0.7 (Bennett & Harvey 1985) and these values bracket the exponent for eye mass on body mass. For species where both brain mass and metabolic rate have been measured, they are linearly related. One can argue, therefore, that the masses of the brain and eye are linked by a dependency on metabolic rate, either throughout life or during development (Martin 1981; Bennett & Harvey 1985).

We now consider the possibility that the eye and brain are scaling with similar exponents because they share the same sensory information (Jerison 1973). A larger eye might require a larger brain to process the extra information it captures. Alternatively, the limited processing ability of the brain could set the dimensions of the eye. To evaluate these possibilities we must consider the relationship between the mass of the eye and the quantity of pictorial information that it gathers. The amount of raw, unprocessed information gathered by a diurnal eye increases in proportion to the number of discrete spatial samples (pixels) on the retina (Laughlin 1998). The number of pixels increases in proportion to retinal area, which is (eye mass)$^{0.67}$. Consequently, a brain whose mass increases in proportion to available information scales with a lower exponent than eye mass. We note that the optic lobes of birds, whose function is to receive direct retinal input and process it pictorially, scale against body mass with an exponent that is 25% less than the brain as a whole (Bennett & Harvey 1985, their Appendix and table I). This lower exponent suggests that the optic lobes are increasing in proportion to raw retinal information, but the rest of the brain is not.

A third factor influencing the mass of the eye is the size of the skull. We find that the lineal dimensions of the skull vary in exact proportion to eye diameter (figures 3 and 4) and birds' eyes so completely fill the skull that they almost touch in the midline (Walls 1942). Aerodynamic, mechanical and physiological constraints on head size (e.g. drag, balance, neck support and blood supply) could necessitate the minimization of the skull and the tight packing of the eye. These constraints would also limit the size of the brain, so causing the skull, the eye and the brain to scale similarly.

In conclusion, there is a well-formed allometric relationship between eye size and body mass in birds. In the present data the exponent of *ca.* 0.67 is consistent, both over the full range of body weights and among different orders. However, we cannot explain this simple exponent in terms of a balance between benefits and costs that scale dimensionally with eye and body size. The scaling exponent does not verify the ecological hypothesis that resolution is proportional to flight speed, but our data does support the common supposition that birds have well developed eyes to cope with the visual demands that come with flight. Other ecological and behavioural factors are clearly important in determining eye size. By comparing the allometric relationships within particular families with the relationship for birds in general we confirm (Walls 1942; Martin 1985) that raptors have large eyes, presumably for acuity and owls have large eyes, presumably for sensitivity. The allometric relationship between eye mass and body mass suggests a number of additional factors. The eye scales to body mass with an exponent similar to brain mass and metabolic rate. These similarities suggest two propositions; either metabolic rate limits both the eye and brain or metabolic rate limits brain mass and brain mass limits eye mass by limiting perception. Because we find that eye diameter and skull size increase in strict proportion, mechanical, aerodynamic and physiological constraints could also be limiting the eye and brain via the size of the head. A more detailed analysis of variations within and between taxonomic, ecological and morphological groups will be required to determine the contributions that these factors and phylogenetic constraints make to determining eye size in birds.

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